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ALLOZYMIC STUDY OF THE RELATIONSHIPS OF PHYLLODERMA AND FOUR SPECIES OF PHYLLOSTOMUS

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The family Phyllostomidae, New World leaf-nosed bats, embraces a diversity of species occurring primarily in tropical and subtropical regions. Currently there are six recognized subfamilies, 49 genera, and approximately 137 species (Jones and Carter, 1976). Evolutionary relationships within the family are complex and different data sets (morphology, karyology, immunology, and protein electrophoresis) often do not indicate identical relationships. A close relationship between the two genera *Phyllostomus* and *Phylloderma* has been recognized based on morphological (Williams and Genoways, 1980), chromosomal (Baker, 1979), and biochemical characters (Honeycutt and Sarich, 1987).

The genus *Phyllostomus* includes four species, *P. discolor, P. hastatus, P. elongatus,* and *P. latifolius.* Three species are geographically widespread (Fig. 1), occurring from southern México throughout much of northern South America, whereas *P. latifolius* has a restricted distribution, occurring only in southeastern Colombia, and in southern Guyana and Suriname (Jones and Carter, 1976). Relationships within and among the species are not well understood. *Phylloderma*, on the other hand, is a monotypic genus with a geographic range from southern México to northern South America (Jones and Carter, 1976). Several recent genetic studies of other genera of bats have indicated that some geographically widespread species actually

may be comprised of two or more biological species (Arnold *et al.*, 1983; Baker *et al.*, 1985, 1988).

This study was designed to examine the relationships within and among the four species of *Phyllostomus* and the single species of *Phylloderma*. We provide genetic data from protein variation to evaluate (1) the status of *Phylloderma* as a distinct genus, (2) the relationships among the species of *Phyllostomus*, and (3) the magnitude of divergence that distinguishes geographically widespread samples within a species.

Methods and Materials

Bats were collected with mist nets from natural populations. Immediately after sacrifice, liver, kidney, and heart samples were removed and frozen in liquid nitrogen. Tissue preparation and starch-gel electrophoresis were similar to those methods of Selander *et al.* (1971) and Harris and Hopkinson (1976). The following 28 presumptive loci were examined (nomenclature and abbreviations follow Harris and Hopkinson, 1976): aconitase 1 (Acon-1), acid phosphatase (Acp), alcohol dehydrogenase (Adh), albumin (Alb), aldolase (Ald), adenylate kinase (Ak-1), creatine kinase 1, 2, 3, 4 (Ck-1, Ck-2, Ck-3, Ck-4), diaphorase (Dia), glyceraldehyde phosphate dehydrogenase (Gapdh), glucose dehydrogenase (Gdh), α-glycerophosphate dehydrogenase (α-Gpd), glucose phosphate isomerase (Gpi), glutamate oxaloacetate transaminase (Got-1, Got-2), isocitrate dehydrogenase (Icd-1, Icd-2), lactate dehydrogenase (Ldh-1, Ldh-2), malate dehydrogenase (Mdh-1, Mdh-2), mannose phosphate isomerase (Mpi), nucleoside phosphorolase (Np), peptidase-B (Pep-B), and superoxide dismutase (Sod-1, Sod-2).

Loci were designated numerically with "1" being the most anodally migrating isozyme of an enzyme and the more cathodal loci given increasingly larger numbers. Allozymes of a given locus were designated alphabetically with "a" representing the most anodal allele with subsequent cathodal alleles given subsequent letters.

The allelic data were used in a cladistical analysis to evaluate phylogenetic relationships (Baverstock *et al.*, 1979; Patton *et al.*, 1981). The particular cladistical approach used was a locus-by-locus analysis where patterns of allele variation were compared to multiple outgroups (Patton *et al.*, 1981). *Macrotus waterhousii*, *Trachops cirrhosus*, and *Chrotopterus auritus* were used as outgroups in this analysis. An allele shared between one or more

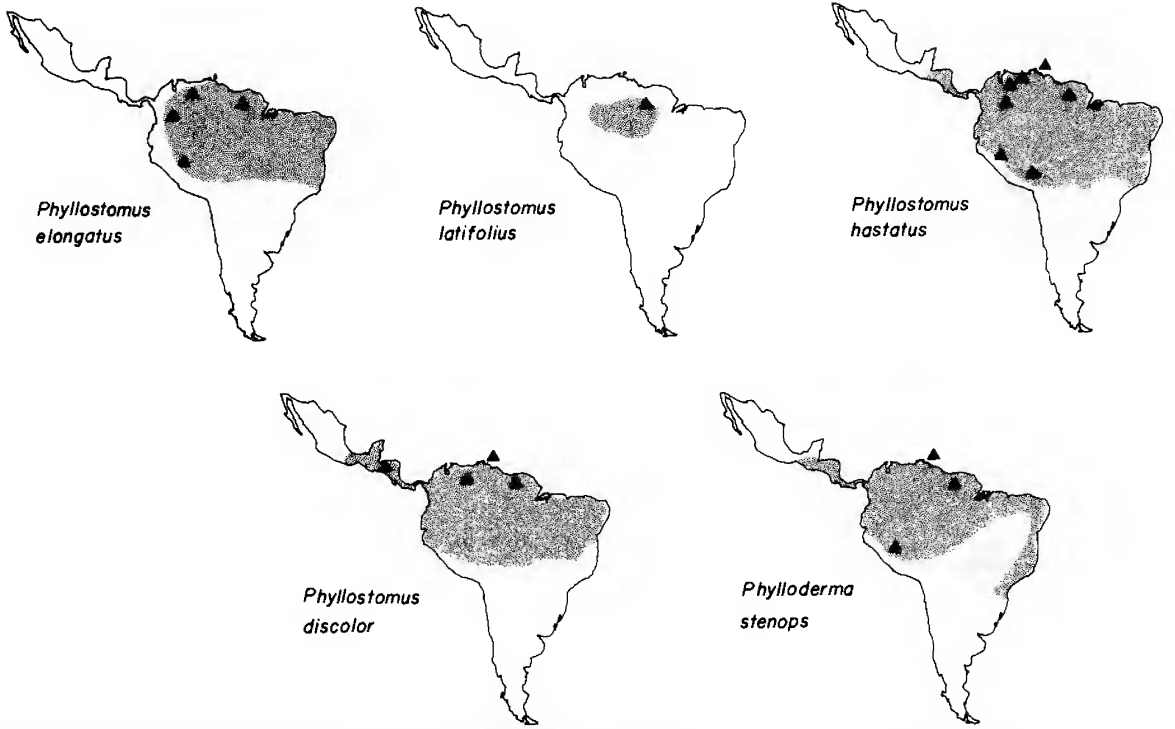

FIG. 1.—Geographic distribution for the four species of *Phyllostomus* and *Phylloderma stenops* from southern México to South America. Triangles indicate localities from which samples were examined in this study.

of the outgroup taxa and *Phylloderma* or one or more of the species of *Phyllostomus* was considered pleisiomorphic for the common ancestor of *Phyllostomus* and *Phylloderma*, thus establishing polarity for the remaining variants in the ingroup.

Phylogenetic relationships between taxa also were evaluated by analyses of genetic distances calculated from the allelic data (Rogers, 1972). Two types of analyses were performed, UPGMA using Rogers' distance values (Sneath and Sokal, 1973) and Fitch and Margoliash (1967) using Rogers' (1972) distance values. Fitch-Margoliash analysis was implemented from PHYLIP using the FITCH option (Felsenstein, 1982).

Specimens Examined

Bats of the genera *Phyllostomus* and *Phylloderma* are geographically widespread in southern Central America and northern South America. Geographic localities of populations sampled during this study are shown in Figure 1. Voucher specimens are housed at Carnegie Museum (CM), Texas A&M University (TAM), Texas Tech University (TTU), El Departemento de Fauna Collection in Caracas, Venezuela (DF) or El Museo Nacional de Historia Natural de Colombia (MNC). Specific localities for specimens are listed below, in parenthesis are TK or AK numbers, which reference laboratory tissue samples to voucher specimens. Museum acronyms of voucher specimens follow the TK or AK number.

Phyllostomus discolor (13).—Honduras: Valle, 2.6 mi. W, 10.8 mi. S Jícaro Galán (AK 9566 TAM, 9582 TAM, 9588 TAM). Trinidad: Nariva Co., San Rafael Ward, Arena Reserve (TK 25126 CM); St. George Co., Arima Ward, 4 mi. N Arima (TK 25250 TTU), SIMLA research station (TK 25043 TAM, 25044 TAM, 25045 TAM). Venezuela: Guarico, 45 km. S Calabozo, Hato Masaguaral (TK 15129 TTU, 15130 TTU, 15104 TTU, 15135 DF). Suriname: Saramacca, Raleigh Falls, 04° 44′N, 56° 12′W (TK 10214 CM).

Phyllostomus elongatus (12).—Colombia: Meta, Villavicencio, El Hachón (TK 16049 MNC). Venezuela: Guarico, 45 km. S Calabozo, Hato Masaguaral (TK 15133 TTU, 15158 TTU, 15212 DF, 15270 DF, 15271 DF). Suriname: Saramacca, Raleigh Falls, 04° 44′N, 56° 12′W (TK 10211 CM, 10212 CM, 10231 CM); Brokopondo, Brownsberg Nature Park, 2 km. W, 8 km. S Brownsweg, 04° 55′N, 55° 11′W (TK 10445 CM, 10446 CM). Peru: Huánuco, 2 km. S Tingo María (TK 22900 CM).

Phyllostomus hastatus (17).—Columbia: Meta, Villavicencio, El Hachón (TK 16060 MNC, 16061 MNC). Venezuela. Miranda, Parque Nacional Guatopo, Agua Blanca (TK 15045 DF, 15046 DF); Guarico, 45 km. S Calabozo, Hato Masagural (TK 15276 TTU). Trinidad: Nariva Co., 3 mi. N, 7 mi. E Ecclesville, Nariva Swamp (TK 25066 TTU, 25068 TTU, 25070 TTU). Suriname: Saramacca, Raleigh Falls, 04° 44′N, 56° 12′W (TK 10206 CM): Voltzberg, 04° 40′N, 50° 12′W (TK 10288 CM); Brokopondo, Rudi Kappeluliegueld, 03° 47′N, 56° 08′ W (TK 10479 CM); Commewijne, Nieuwe Grond Plantation, 05° 53′N, 54° 54′W (TK 10374 CM). Peru: Huánuco, 6 km. N Tingo María (TK 22590 CM), 1 km. S Tingo Maria (TK 22645 CM, 22647 TAM, 22648 TAM). Bolivia: La Paz, 1 mi. W Puerto Linares (TK 14534 TTU).

Phyllostomus latifolius (6).—SURINAME: Brokopondo, 1 km. N Rudi Kappeluliegueld, 03° 48′N, 50° 08′W (TK 11216 CM, 11218 CM), 3 km. SW Rudi Kappeluliegueld, 03° 46′N, 56° 10′W (TK 11269 CM, 11278 CM), 1.5 km. W Rudi Kappeluliegueld, 03° 47′N, 56° 10′W (TK 11301 CM, 11302 CM).

Phylloderma stenops (6).—TRINIDAD: St. George Co., 4 mi. N Arima (TK 25248 CM). SURINAME: Saramacca, Raleigh Falls, 04° 44′N, 50° 12′W (TK 10213 CM); Brokopondo, Brownsberg Nature Park, 2 km. W, 8 km. S Brownsweg, 04° 55′N, 50° 11′W, (TK 10459 CM), 3 km. SW Rudi Kappeluliegueld, 03° 46′N, 56° 10′W (TK 11275 CM, 11321 CM). PERU: Huánuco, 9 km. S, 2 km. E Tingo María (TK 22935 CM).

Chrotopterus auritus (2).—SURINAME: Saramacca, Raleigh Falls, 04° 44′N, 50° 12′ W (TK 10210 CM); Nickerie, Sipaliwini Airstrip (TK 10137 CM).

Trachops cirrhosus (1).—TRINIDAD: Mayaro, 1 mi. S, 2 mi. W Guayaguayare (TK 25242 CM).

Macrotus waterhousii (2).—MEXICO: Guerrero, 31 mi. SW Iguala on Hwy. 95 (TK 4838 TTU, 4839 TTU).

RESULTS

Of the 28 presumptive loci that were examined, four (Mdh-1, Gapdh, Ck-4, and Acp) were monomorphic for all individuals of *Phyllostomus, Phylloderma,* and the outgroups (*Trachops cirrhosus, Macrotus waterhousii,* and *Chrotopterus auritus*). Four additional loci (Mdh-2, Ck-2, Ck-3, and Sod-1) were monomorphic across all individuals of the ingroups (*Phylloderma* and four species of *Phyllostomus*). Additionally, a single allele for Ldh-2 was present in the four species of *Phyllostomus,* and *Phylloderma* was fixed for an alternate allele. The 24 variable loci and the frequencies of their respective alleles within the taxa examined are presented in Table 1. Rogers' (1972) genetic distance and Nei's (1972) genetic distance for all pairwise comparisons of taxa are given in Table 2. The results of a UPGMA clustering analysis of Rogers' distance values within and between taxa are depicted in Figure 2. This provides a representation of the extent of geographic variation between samples of each species as well as the phenetic association of species examined. Figure 3 shows the result of the Fitch-Margoliash analysis of genetic distances (Rogers, 1972) between taxa, with the tree rooted in *Macrotus, Trachops,* and *Chrotopterus.* The results of a locus-by-locus analysis using outcrops is shown in Figure 4.

DISCUSSION

Geographic variation.—All populations within a species are genetically similar to one another (Table 1 and Figs. 1 and 2). Populations from Trinidad, an island off the coast of Venezuela,

TABLE 1.—*Allozyme designations and figures for samples of* Phylloderma *and* Phyllostomus *and outgroup taxa. For species in which more than one allele is present, the number in parenthesis immediately following the allele designation is the frequency of that allele. Loci and allele designations are identified in text. Four loci were monomorphic for all specimens (MDH-1, GAPDH, CK-4, and ACP).*

	ACON-2	ADH	ALB	ALD	AK-1	CK-1	CK-2	CK-3	DIA	GDH	α-GPD	GPI	GOT-1	GOT-2	ICD-1	ICD-2	LDH-1	LDH-2	MDH-2	MPI	NP	PEP-B	SOD-1	SOD-2
											Phylloderma stenops													
Suriname	B	C	B	B(.5) D(.5)	B	D	B	B	B(.5) D(.5)	A(.5) B(.5)	A(.5) B(.5)	B	B	B	D	A	A	C	B	B	B	B	B	A
Trinidad	B	C	B	A	B	D	B	B	B(.5) D(.5)	A	A	B	B	B	D	A	A	C	B	B	B	B	B	A
Perú	B	C	B	B	B	D	B	B	B(.5) D(.5)	A	A	B	B	B	B(.5) D(.5)	A	A	C	B	B	B	B	B	A
											Phyllostomus discolor													
Suriname	C	D	C	B	B	C	B	B	B(.5) C(.5)	B	A	C	B	B	C(.5) D(.5)	A	A	A	B	B(.5) C(.5)	B	D	B	D
Venezuela	C	D	C	A(.25) B(.75)	B	C	B	B	B(.75) C(.25)	B(.75) C(.25)	A	C	B	B	C	A	A	A	B	C	B	B(.25) D(.75)	B	D
Trinidad	C	D	C	A(.4) B(.4) D(.2)	B	C	B	B	B	B(.4) C(.6)	A	C	B	B	C	A(.8) B(.2)	A(.8) B(.2)	A	B	C	B	B(.2) D(.8)	B	D
Honduras	C	D	C	B	B	C	B	B	B	B(.54) C(.46)	A	C	B	B	C	A	A	A	B	C	B	D	B	D
											P. elongatus													
Suriname	C	C	B	B	B	B(.2) C(.8)	B	B	B	D(.4) E(.6)	B(.4) C(.6)	B	E	A	D	A	A	A	B	C	A	C	B	C
Venezuela	C	C	B	B(.2) C(.2) D(.6)	B	B(.25) C(.75)	B	B	B	D(.2) E(.8)	B(.8) C(.2)	B	E	A	D	A	A	A	B	C	A	C	B	C
Perú	C	C	B	B	B	B	B	B	B	D	B	B	E	A	D	A	A	A	B	C	A	C	B	C
Colombia	C	C	B	A	B	C	B	B	B	E	B	B	E	A	D	A	A	A	B	C	A	C	B	C

TABLE 1.—*Continued.*

										P. latifolius													
Suriname	A	C	B	D	B	C	B	B	B(.4) C(.6)	B(.17) C(.5) D(.33)	A(.8) B(.2)	B	C	A	D	A	A	A	B	D	B	A	B	B
										P. hastatus													
Suriname	B	C	B	A(.5) B(.5)	C	B	B	B	A(.12) B(.5) C(.38)	D(.5) E(.5)	B	A	E	B	D(.25) E(.75)	A(.75) B(.25)	A	A	B	C	A	B	B	D
Venezuela	B	C	B	A	C	C(.67) E(.33)	B	B	A(.33) B(.33) C(.33)	D(.33) E(.67)	A(.67) B(.33)	A	E	B	E	A	A	A	B	C	A	B	B	D
Colombia	B	C	B	A	C	B(.5) C(.5)	B	B	A(.25) C(.75)	E	A	A	E	B	E	A	A	A	B	C	A	B	B	D
Bolivia	B	C	B	A	C	B	B	B	B(.5) C(.5)	E	A	A	E	A	D(.5) E).5)	A	A	A	B	C	A	B	B	D
Perú	B	C	B	D	C	B	B	B	B(.12) C(.88)	E	A(.75) B(.25)	A	E	B	E	A	A	A	B	C	A	B	B	D
Trinidad	B	C	B	A(.5) D(.5)	C	A(.5) B(.5)	B	B	B(.83) C(.17)	E	A	A	E	B	E	A	A	A	B	C	A	B	B	D
										Outgroups													
Chrotopterus	A	A	A(.5) B(.5)	D	B	B	A	B	B	A(.5) B(.5)	A	B	A	B	D	A	A	B	B	B(.5) C(.5)	A	C	A	D
Trachops	A	C	B	C	A	E	A	A	C	D	A	A	B	A	A	A	A	B	C	C	A	D	D	D
Macrotus	A	B	B	E	B	E	C	B	C	D	A	B	D	B	B(.25) D(.75)	A	A	C	A	A	A	E	C	D

TABLE 2.—*Nei's distance (above) and Rogers' distance (below) values for species of* Phylloderma *and* Phyllostomus.

	stenops	*hastatus*	*elongatus*	*discolor*	*latifolius*	*Chrotopterus*	*Trachops*	*Macrotus*
Phylloderma								
stenops	—	0.47	0.48	0.50	0.43	0.56	0.89	0.69
Phyllostomus								
hastatus	0.38	—	0.36	0.49	0.53	0.66	0.73	0.77
elongatus	0.39	0.32	—	0.50	0.36	0.53	0.78	0.80
discolor	0.41	0.40	0.40	—	0.52	0.66	0.85	0.89
latifolius	0.37	0.42	0.32	0.42	—	0.58	0.74	0.69
Chrotopterus	0.45	0.51	0.43	0.49	0.45	—	0.63	0.57
Trachops	0.59	0.52	0.55	0.58	0.51	0.48	—	0.63
Macrotus	0.50	0.55	0.56	0.59	0.51	0.45	0.50	—

are similar to mainland populations and the Gulf of Paria does not appear to represent a strong barrier to dispersal in these bats. In some other studies of genetic variation in geographically widespread samples of bats (*Tonatia* and *Micronycteris* of the Phyllostomidae—Arnold *et al.*, 1983, and *Rhogeessa* and *Lasiurus* of the Vespertilionidae—Baker *et al.*, 1985, 1988), there was evidence that at least four taxa previously recognized as a single species actually represented two or more biological species (*Tonatia nicaragua, Rhogeessa tumida, Lasiurus borealis,* and *L. ega*). Our data are compatible with the conclusion that species of *Phyllostomus* and *Phylloderma* represent widespread taxa with minimal geographic differentiation, rather than a species complex as seen, for example, in the *Rhogeessa tumida* complex (Baker *et al.*, 1985). However, genic data that fail to document fixed differences between populations do not preclude the possibility that two biological species were sampled. This point has been made clear in the data presented by Koop and Baker (1983) in a study of another genus of phyllostomid bats (*Artibeus*), where no fixed allelic difference could be demonstrated that accompanied speciation documented by studies of cranial and external morphology. Nonetheless, the available morphological, genic, and chromosomal data (Baker, 1979) are all compatible with the conclusion that *Phyllostomus discolor, P. elongatus, P. hastatus,* and *Phylloderma stenops* respectively represent widely distributed species.

Species definition.—All five species of the *Phyllostomus-Phylloderma* group are distinguishable from each other by several

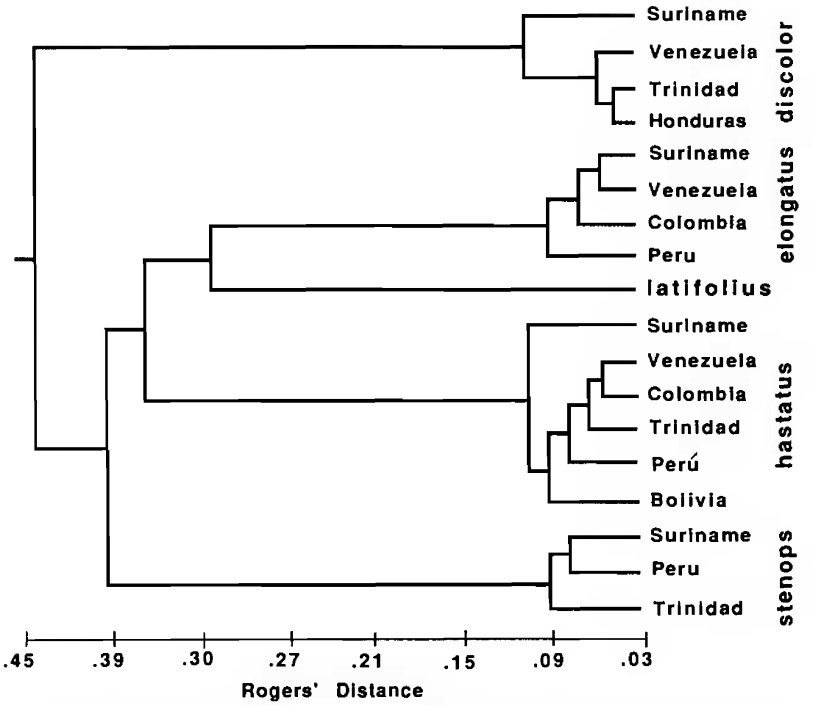

FIG. 2.—Phenogram generated from Rogers' (1972) genetic distance values using a UPGMA clustering analysis (Sneath and Sokal, 1973). Cophenetic correlation value is 0.963.

fixed electromorphs that are unique to a given species (Table 1 and Fig. 2). The specific status of *P. latifolius* relative to *P. elongatus* has been debated (Jones and Carter, 1976). The paucity of specimens of *P. latifolius* and *P. elongatus* from sympatric localities has hindered the determination of the relationship between these two species. Valdez (1970:121) wrote, "The anatomical similarity of *P. elongatus* and *P. latifolius* indicates they are closely related if not conspecific; however because of the disparity between the series of *P. latifolius* and the samples of *P. elongatus* from Guyuana, they are treated here as distinct species." In this study, samples of *P. elongatus* and *P. latifolius* from Suriname (Brokopondo) are from geographically adjacent localities and the two species differ by several fixed allelic differences at these localities (Table 1 and Fig. 2). The two species have been recorded in sympatry in this area (Williams and Genoways, 1980). Data from protein electrophoresis (this study) and albumin immunological distances (Honeycutt and Sarich,

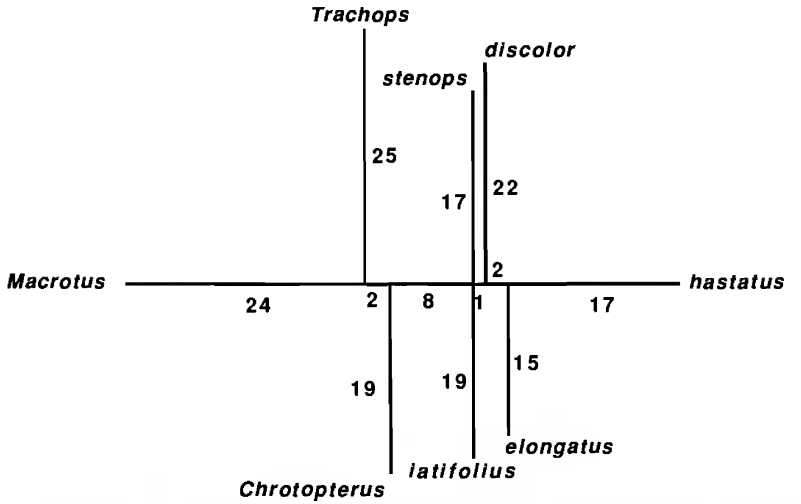

FIG. 3.—Phylogeny of *Phyllostomus* and *Phylloderma* based on a Fitch-Margoliash (1967) analysis of Rogers' (1972) genetic distances. The numbers along the lines represent the amount of change apportioned to each lineage relative to the outgroups. Each branch length unit is equal to 0.1 distance units (Rogers, 1972).

1987) between the two species document the genetic distinctiveness of them and provide unequivocal evidence that *P. latifolius* and *P. elongatus* are distinct species.

In contrast to the low levels of geographic variation found within species, the level of genetic distinctiveness among species is high relative to those found in some genera such as *Artibeus* (Koop and Baker, 1983) and *Monophyllus* (Baker *et al.*, 1981). If the molecular clock hypothesis is accepted, this would indicate that speciation events giving rise to the extant species occurred much earlier in *Phyllostomus* than in *Artibeus* and *Monophyllus*. A similar pattern of divergence in genic similarity has been observed in some other phyllostomine genera (*Micronycteris* and *Tonatia*—Arnold *et al.*, 1983), which leads to the hypothesis that most genera in this currently recognized subfamily are relatively divergent from each other and that most species within this subfamilial complex may have arisen earlier than some of those found in the Stenodermatinae (Koop and Baker, 1983) and the Glossophaginae (Baker *et al.*, 1981). Alternatively, differentiated rates of molecular evolution (Arnold *et al.*, 1982) could produce similar results to those described for these phyllostomines and *Artibeus* and *Monophyllus*.

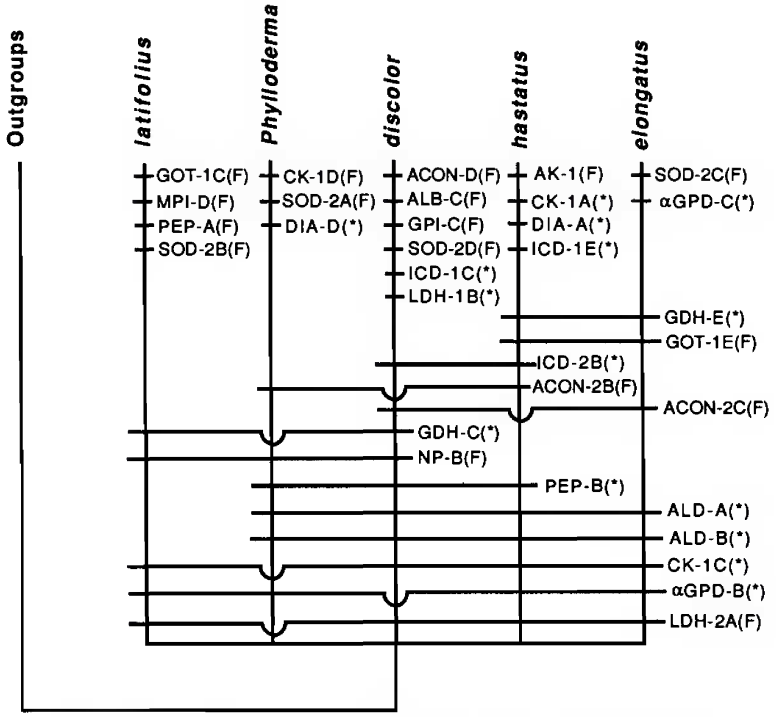

FIG. 4.—Shared derived and unique character states of *Phylloderma* and four species of *Phyllostomus* using *Macrotus waterhousii*, *Trachops cirrohus*, and *Chrotopterus auritus* as outgroups. Although the greatest number of shared derived character states unite *hastatus* and *elongatus*, and *latifolius* shows the fewest derived character states, we have represented these taxa as unresolved because the complex system must involve numerous reversals, convergencies, or primitive polymorphic states. F = fixed for allele in sample, asterisk = polymorphs for this allele in sample.

Interspecific relationships—Providing unambiguous resolution to the possible relationships of taxa within genera often has been extremely difficult and this appears to be true for members of the *Phyllostomus-Phylloderma* complex. Valdez (1970) reviewed the morphological characteristics of the species and, although he proposed a close relationship for *P. elongatus* and *P. latifolius*, he concluded other relationships were not well defined by cranial and external characteristics. The genetic data from protein electrophoresis also fail to provide unequivocal resolution to interspecific relationships. The UPGMA clustering analysis (Fig. 2) indicates a close relationship between *P. elongatus* and *P. latifolius*, with *P. hastatus* joining this group at a genetic

distance of about 0.35. *Phylloderma stenops* is the next most closely related taxon and *P. discolor* is the most basal member of the group. However, the Fitch-Margoliash analysis (Fig. 3) indicates a weak association of *hastatus-elongatus*, whereas *latifolius, stenops,* and *discolor* are unresolved at the base of the tree. Within the genus *Phyllostomus,* taxa are united by less than four distance units with the remainder of the distance partitioned on branches of individual species (Fig. 3). A locus-by-locus cladistical analysis (Fig. 4) also fails to provide resolution to species relationships where the branching sequence order is confused by either reversals, convergent evolution, or polymorphism in the ancestral stock. When the results of all three of these analyses (UPGMA, Fitch-Margoliash, and locus-by-locus cladistics using outgroups for rooting) are compared to immunological distance data (Honeycutt and Sarich, 1987), there is little resolution of the unresolved multichotomy of all five species of the *Phyllostomus-Phylloderma* complex. The data from *Phyllostomus* may be explained best by the hypothesis that the five species (including *Phylloderma stenops* arose at approximately the same time.

Should *Phylloderma* be recognized as a distinct genus relative to *Phyllostomus*? From the protein data, the inclusion of *Phylloderma stenops* in the genus *Phyllostomus* would not add significant genetic variation to that already present in the genus. *Phylloderma* has three unique alleles not found in any species of *Phyllostomus* nor in any outgroup taxon and one of these alleles occurs in a polymorphic state (Table 1 and Fig. 4). Each of the four species of *Phyllostomus* has an equal number of autapomorphies (Fig. 4). Little additional variation in characters would be added for gross morphology (Miller, 1907), karyology (Patton and Baker, 1979), or albumin immunology (Honeycutt and Sarich, 1987) if *Phylloderma* were included in the genus *Phyllostomus.* G- and C-banded chromosome patterns of *Phylloderma stenops* are identical to those of *Phyllostomus hastatus* (unpublished data). In fact, both genetic data sets (protein electrophoresis, this study, and albumin immunology, Honeycutt and Sarich, 1987) are in agreement in that the removal of *Phyllostomus discolor* and the inclusion of *Phylloderma stenops* in a single genus would minimize the amount of variation within the genus over any combination of four species. The amount of reduction of genetic variability would, however, be small. Therefore, it is better to recognize *Phylloderma stenops* as cogeneric with

Phyllostomus in order to emphasize the close affinities between the two taxa than to recognize a monotypic genus that stands alone and obscures this genetic relationship. Therefore we propose that *Phyllostomus* be composed of five species (*discolor, elongatus, hastatus, latifolius*, and *stenops*) and that no subgenera be recognized.

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